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STEVEN F. BARGHOORN[1]

ABSTRACT

Two previously undescribed skulls of *Vespertiliavus* Schlosser have occasioned close examination of emballonurid and other chiropteran cranial morphology in order to assess its usefulness for elucidating phylogenetic relationships within the Emballonuridae. A Ludian to Sannoisian age for the fossils, from the Quercy Phosphorites of France, suggests that many features of the basicranium and ear region, seen also in closely related genera, are ancient and have changed little in the course of later Tertiary evolution. The distribution of skull characters leads to a somewhat tentative hypothesis of relationships, allying the fossil genus more closely to some living emballonurids than to others. Skull characters can be used to relate these and other chiropterans, but with difficulty.

INTRODUCTION

Compared with many other mammalian groups, new finds of well-preserved, pre-Pleistocene bats are rare in paleontology. The fossil record has seemingly left students of chiropteran evolution three times short-changed. For one, coverage is scanty and uneven: with a recent diversity of about 130 genera of bats recognized (Koopman and Jones, 1970), only a little more than 30 genera are known from the pre-late Pliocene Tertiary (Romer, 1966), and the majority of these are from Europe. For another, the record shows no intermediate stages in the origin of the order: the oldest material which is complete enough to assign to the bats with certainty shows only that (micro)chiropteran morphology was in general distinctly established in the early Tertiary (see Jepsen, 1970). Paleocene and Eocene material which is not distinctly chiropteran, if indeed it does belong to the earliest bats, has yet to be distinguished and removed from the contemporaneous insectivores (particularly shrews) and possibly primates (McKenna, personal commun.). Thirdly, within the order the record offers no progressive evolutionary stages that might be used to delineate the taxonomy and illustrate the development of the present diversity of bats against the framework of time. For many taxa morphology has changed little during the later Tertiary; some Eocene and Oligocene material has been acceptably referred to

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living genera. More immediately than workers in other groups, then, bat paleontologists are forced to base their methods on comparative morphology, without recourse to stratigraphic arguments. Good fossil material can both extend the range of known morphology and help clarify previously poorly known character distributions and associations.

The present paper describes two new specimens of emballonurid bats from the Quercy Phosphorites, both well-preserved skulls referred to the genus *Vespertiliavus* Schlosser. Other material, also including skulls, was described by Revilliod in 1920. Apart from diagnosing *Vespertiliavus* as a primitive member of the Emballonuridae, Revilliod did not consider relationships among all the genera of the family although his conclusions were based on careful examination of morphology. An attempt is made here to elucidate those relationships; in general Revilliod's conclusions on *Vespertiliavus* are supported, although difficulties with them are pointed out.

Cladistic analysis is the method of phylogenetic reconstruction used here. This has been extensively discussed by Hennig (1966), Brundin (1966, 1972), Nelson (1973), and others, and its theoretical basis need not be defended further in this paper. It is important, however, that the nature of a cladistic hypothesis of relationships makes it possible to state explicitly its internal inconsistencies—viz., character distributions that conflict with the hypothesis as proposed. Conflicting character distributions imply that at least one of the features being investigated has been acquired independently in more than one group and, depending on the hypothesis of relationships preferred, is not homologous among forms that appear to possess it. Presumably any character (in the most general sense) can be used to adduce or test such a hypothesis. This has been assumed in making observations on the material of this study and in formulating the morphology in terms of the characters presented in part in table 2. In fact, at a higher level of taxonomy involving morphologically more divergent forms, many of these characters might be considered trivial beside more striking contrasts and unique features. This does not, however, affect their potential applicability to the problem at hand, namely, relationships within this one family of bats. The outcome of the study seems to show, as discussed later, that these characters do not enable one to discern the relationships easily. The several alternative phylogeny reconstructions all imply that emballonurid (and, generally, chiropteran) evolution has involved to a considerable degree the independent acquisition of characters.

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Institutional Abbreviations

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History
AMNH (Mam), Department of Mammalogy, the American Museum of Natural History
PU, Geology Museum, Princeton University

Figure Abbreviations

ab, ? line of attachment of membranous bulla
ac, anterior cingulum
alf, alveolar foramina
al + of, confluent anterior lacerate plus optic foramen
app, anterior process of petrosal
bp, basisphenal pit
cf, condyloid fossa
cpb, cochlear process of basisphenoid
egl, ectotympanic groove lateral part
egm, ectotympanic groove medial part
er, epitympanic recess
fl VII, flange over path of VII
fme, foramen for ?medial entocarotid artery

fmma, separate opening associated with foramen ovale
fo, foramen ovale
fov, fenestra ovalis
fpg, postglenoid foramen
frisa, foramen for ?ramus inferior of stapedial artery
frot, fenestra rotundum
f ?v, foramen for ?vein
g, grooves in interpterygoid trough
gmp, groove medial to petrosal
g VII, groove for VII lateral to promontorium
hb, hypoconal basin
in, internal nares
jf, jugular foramen
lap, lamina extension of petrosal
lbp, lateral basal (= pterygoid) pit
lc, lingual cingulum
lf, lacrimal foramen
mal, malleus
mc, median canal
mca, metacrista
me, metacone
"mes," "mesostyle"
mf, maxillary foramen
mr, molar roots
ms, mesostyle
msn, median septum of nares
mt, metastyle
occ, occipital condyle
pa, paracone
paca, paracrista
pars mas, pars mastoideus of petrosal
par proc, paroccipital process
pas, parastyle
pf, pterygoid flange
pgp, postglenoid process
pob, postorbital bar
pop, prominence on promontorium
pp, pterygoid process
ppf, posterior palatine foramen
ppp, posterior process of petrosal
pr, protocone
prca, precentrocrista
prem, premaxillary
prom, promontorium
pt, tubercle on promontorium
ptca, postcentrocrista
ptp, posttympanic process
pyf, pyriform fenestra
sf, stapedial fossa
spf, sphenopalatine foramen
st, stylocone

SYSTEMATICS

ORDER CHIROPTERA

SUBORDER MICROCHIROPTERA

SUPERFAMILY EMBALLONUROIDEA

FAMILY EMBALLONURIDAE DOBSON, 1875

VESPERTILIAVUS SCHLOSSER, 1887

Vespertiliavus cf. *bourguignati* Filhol, 1877, p. 45, figs. 5-8.

Referred Specimen. AMNH 55349, skull, without jaws, complete except for parts of dentition and middle ear ossifications; somewhat damaged.

Locality and Horizon. Mouillac, near Caylux, Quercy Phosphorites, south central France.

Age. Late Eocene (Ludian) or early Oligocene (Sannoisian) (Thaler and Hartenberger, 1974).

Diagnosis. Filhol, 1877, pp. 45-48; but see Discussion below.

Measurements. See table 1.

Discussion. The specific assignment of AMNH 55349 is not entirely clear, pending revision of the genus. Revilliod (1920) was the first to describe skulls of *Vespertiliavus*, of which he had two apart from fragments, one referred to *V. bourguignati*, the other designated *V. schlosseri.* These and the other two species, *V. wingei* and *V. gracilis*, Revilliod distinguished largely on the basis of size. But his diagnoses (and other descriptions) give only one measurement of skull material for all: the linear distance from P^1 to M^3 (see table 1, no. 1). AMNH 55349 is larger than Revilliod's species *V. wingei*, the form largest in this measurement, and is in fact smaller than Filhol's type specimen for *V. bourguignati* because its measurement of 11 mm. encompasses only P^1 to M^2 (Filhol, 1877, p. 47). Were size the only character used for specific taxonomy, it would appear that AMNH 55349 might be referred to *V. bourguignati*; and that Revilliod's material for that species was incorrectly referred and belongs to a new species intermediate between *V. wingei* and *V. schlosseri.* Revilliod, concerned largely with the morphology of the genus as a whole, did not give fully comparative treatment of possible species differences. Erection of

a new species for AMNH 55349 at the moment seems unncessary.

Vespertiliavus cf. *schlosseri* Revilliod, 1920, p. 105, pl. I, figs. 9-12.

Referred Specimen. PU 11573 skull, complete except for right canine, right and left P^1, zygomatic arches, ear ossicles, and most cranial roofing bones. Brain endocast, somewhat distorted, visible on left side. Right tympanic preserved, displaced against pterygoid flange. Right premaxillary bone and incisor present.

Locality and Horizon. Bech-barrond, near St. Antonine, Quercy Phosphorites, south central France.

Age. Late Eocene (Ludian) or early Oligocene (Sannoisian).

Diagnosis. Revilliod, 1920, p. 105; but see Discussion below.

Measurements. See table 1.

Discussion. Specific assignment of this material is left open pending revision of the genus; on the basis of size this skull appears closer to *V. schlosseri* than to any other species.

Key to measurements in Table 1

(Revilliod, 1920, pp. 94-95)

1. Linear distance P^1-M^3.
2. Maximum cranial length—back of sagittal crest to anterior border nasals.

TABLE 1
Skull Measurements (in Millimeters) for *Vespertiliavus* and Examples of Closely Related Genera

Measurement Number (see Key)	AMNH 55349	PU 11573	*Vespertiliavus bourguignati* (Revilliod, 1920)	*Vespertiliavus schlosseri* (Revilliod, 1920)	*Saccolaimus peli* AMNH (Mam) 48757	*Taphozous nudiventris* AMNH (Mam) 27391	*Taphozous melanopogon* AMNH (Mam) 107656
1.	11.5	8.6	8.0-8.5	6.8-7.3	9.8	8.3	6.9
2.	27.1	21.3	26.5[a]	22.7	25.8	21.7	18.9
3.	12.4	*b*	*c*	11.4	12.7	13.6	12.9
4.	20.3[d]	17.7	22.5	?18.3[e]	21.0	18.4	15.5
5.	9.5	8.5	9.8	9.5	9.6	6.8	6.0
6.	14.3	*b*	*c*	11.3	13.0	8.1	7.5
7.	7.0	5.7	*c*	6.3	7.0	6.4	6.4
8.	27.8	21.5	*c*	*c*	25.7	22.8	19.4
9.	17.2	*b*	*c*	*c*	20.8	14.9	12.5
10.	12.0[f]	*b*	*c*	*c*	13.2	11.0	10.0
11.	14.9[f]	11.5	*c*	*c*	16.5	13.0	11.1
12.	?6.9[f]	4.9	*c*	*c*	6.5	4.5	5.2
13.	12.3	*b*	*c*	*c*	11.3	8.8	8.0
14.	6.1	5.1	*c*	*c*	7.1	6.1	4.0
15.	14.4[g]	10.5	*c*	*c*	11.5	10.1	8.4
16.	4.0	2.5	*c*	*c*	4.0	2.4	2.6
17.	*b*	*b*	*c*	*c*	10.9	7.9	8.3

[a]"Longeur totale de l'occiput au bord antérieur des alvéoles des C" (Revilliod, 1920, p. 95) not clearly homologous with skull length measured for *V. schlosseri*: "Longeur de l'extrémité postérieure de la crête sagittale à l'extrémité antérieure des naseaux" (p. 94).

[b]Not obtainable accurately from specimen.

[c]Not recorded by Revilliod (1920).

[d]Obscured by remaining matrix.

[e]"Longeur basilaire" (Revilliod, 1920, p. 94): definition unclear.

[f]Evidently affected by distortion as preserved.

[g]Left side; right side distorted.

3. Length sagittal crest.
4. Basal length—median length from posterior edge basioccipital to anterior border maxillary.
5. Median length of bony palate.
6. Snout length—front sagittal crest to anterior border of nasals.
7. Basicranial length—posterior border of basioccipital to level of anterior border of basisphenal pits.

(Smith, 1972, p. 6)

8. Condylobasal length—back of condyle to front of maxillary.
9. Zygomatic breadth—greatest breadth across zygomatic arches.
10. Braincase breadth—maximum breadth.
11. Mastoid breadth—maximum breadth across back of skull.
12. Postorbital breadth—minimum breadth in postorbital constriction.
13. Rostral breadth—maximum breadth between front of circumorbital rims (between lacrimal foramina).
14. Snout breadth—maximum breadth between canines.
15. Alveolar length of tooth row—front canine to M^3.
16. Breadth of postpalatal extension—minimum breadth between bases of pterygoid flanges at level of palate.
17. Depth of braincase—from glenoid fossa vertically to highest point on braincase.

DESCRIPTION

The following description centers primarily on AMNH 55349 and is given to (1) describe the state of preservation of this new fossil material; (2) present in detail certain aspects of chiropteran cranial morphology as exemplified by this skull; and (3) compare this form with two closely related emballonurids (*Taphozous* and *Saccolaimus*[1]) and occasionally with more distantly related forms for purposes of phylogenetic reconstruction. Because of the less well-preserved condition of PU 11573, reference is made to this skull only where it differs significantly from AMNH 55349 and where it exhibits morphology not available from the latter.

Preservation. AMNH 55349 (figs. 1-5) is least deformed in ventral aspect, although the following features are distorted or lost. There is no sign of premaxillaries or incisors. The left canine and all premolars except the last on each side have been broken off at the neck. The palate, pterygoid flanges, condyles, basicranium, and ear regions are all present, although the roof of the basisphenal pits may have collapsed dorsally. The palate is cracked, mostly lengthwise, but with no important displacement of parts. Both pterygoid flanges are cracked and displaced such that what are presumably simple pterygoids appear ambiguously as compound. A sliver of bone is missing from the ventralmost crest of the right pterygoid; the left has been cracked and slightly displaced at its juncture with the palate. Mostly transverse cracking and stepwise displacement have occurred in the bones (basisphenoid and vomer) roofing the internal nares, making interpretation of openings in this area somewhat difficult. The basisphenoid is also cracked in two places between the ear regions, with some displacement; possibly this has been accompanied by slight rotation and settling of the petrosals but both of them are identically placed and no disturbances are apparent in the mastoid regions (see below).

Crushing and breakage have obscured more features in dorsal and lateral aspects (figs. 2, 3). The entire cranium has been flattened, especially posteriorly, though all bone appears to be present. Irregular pieces of bone have settled in places and are covered with thin veneers of matrix in the prepared specimen. On both sides the sphenorbital regions are shattered and dorsoventrally flattened so badly that foramina and other morphology can hardly be made out. It is unlikely that cranial flattening has resulted directly in the broken basisphenoid. The angle between this part of the basicranium and the palate is approximately flat; this is also the case in living *Taphozous* and the condition in the fossil may be an accurate preservation. The septum between the basisphenal pits (see below) appears to have been warped dorsally under pressure applied at the ?hyoid fragment still remaining in the left pit. (The reconstruction of the hyoid elements seems unlikely because of their distorted posi-

[1]*Saccolaimus* is currently recognized as a subgenus of *Taphozous*. Its skull proportions and ossification, and especially auditory bulla morphology render it a distinct and valid taxonomic unit within the Family Emballonuridae, which may be reflected by according it generic status (Koopman, personal commun.). It is ranked as a genus in this paper.

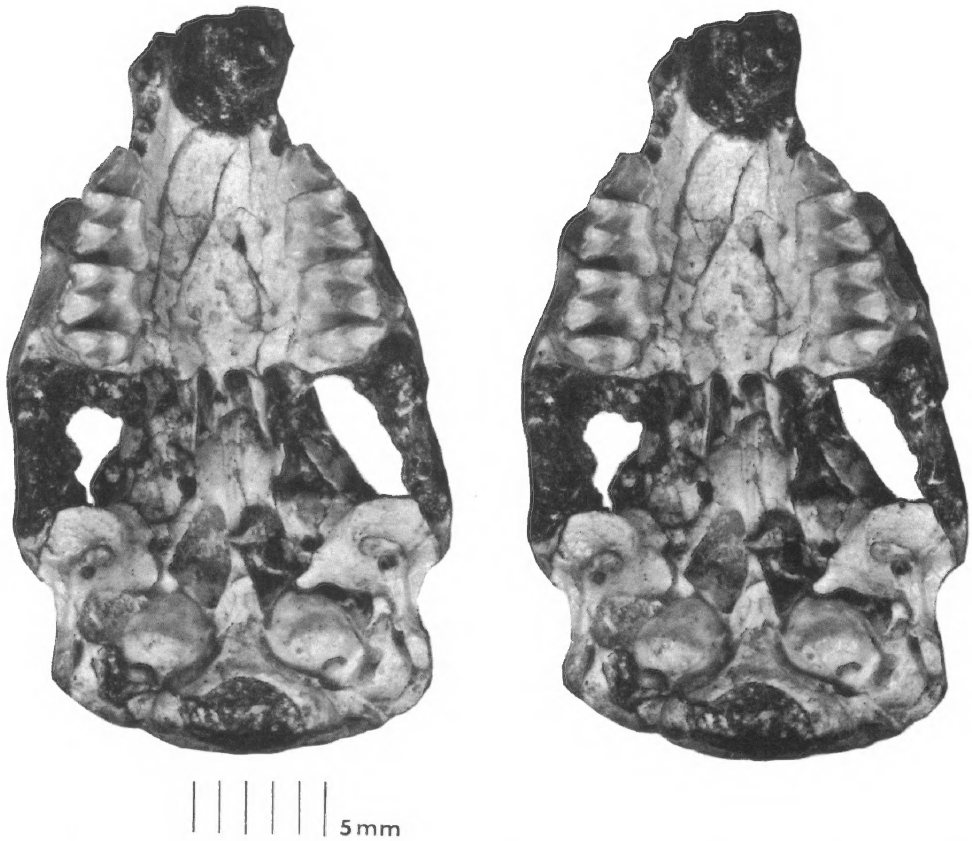

FIG. 1. AMNH 55349. *Vespertiliavus* cf. *bourguignati*. Stereophotographs of skull, ventral view.

tion, and in view of uncertainties in identifying them; much of the matrix of the Phosphorites consists of innumerable unidentifiable bone chips and splinters.)

Both postorbital bars are fully present, presumably in near natural shape; broken at their bases, they are disoriented in the general flattening of the skull. Both zygomatic arches are in complete condition, cracked through at least once each, but with minimal displacement. The right paroccipital process is not in place; a matrix-veneered flange of bone next to the base of it is most likely the broken piece.

In preparation the left ear and mastoid region have been exposed more fully than the right; the right orbit more fully than the left. For structural support matrix has been left surrounding the (left) canine, both zygomatic arches, the dorsoposterior margin of the palate and, in lesser amounts, on the pterygoid flanges. Neither the foramen magnum nor the external narial opening has been excavated. Despite the remaining matrix the morphology has been exposed to be adequately described within the limits of the state of preservation.

Preservation of PU 11573 shows almost no cracking of bone and infilling by matrix. The skull has not been flattened as has the larger fossil, but the cranium and occipital areas show evidence of overall distortion. Much of the roofing bone of the left frontal, parietal, and right occipital areas has been removed and, due to the inflated nature of the cranium, a faithful endocast has been exposed over this area (cf. Descheseaux, 1956, fig. 1, p. 121). The basisphenoid is largely obscured by the displaced tympanic,

but basisphenal pits of characteristic shape and spacing are definitely present. The right ear region shows some morphology of the anterior process of the petrosal not available on AMNH 55349. The sphenorbital region is preserved on both sides. Most significantly, the right premaxillary bone and incisor are preserved.

General Outline. The general outline, indeed the whole morphology of the skull of AMNH 55349, is similar to *Taphozous* (especially *T. nudiventris*), as discussed by Revilliod (1920). Contrasts noted are: size larger by about one-eighth (see table 1) compared with largest *Taphozous* (*Taphozous*) species; "snout," that is, the area anterior to the abrupt broadening of the skull for orbits and cheek teeth, relatively longer and more curved on its dorsal surface; orbits surrounded by sharper, more pronounced rims of the maxillary, lacrimal, and frontal bones. Seen ventrally the line of the cheek in front of the zygomatic arch angles inward more sharply to the preorbital constriction in *Taphozous*, while running nearly straight forward in AMNH 55349. The lambdoid crest runs straighter from right to left side than that in *Taphozous*, in which it merges backward to a common point with the sagittal crest above and behind the foramen magnum. In ventral outline AMNH 55349 and *Taphozous nudiventris* are nearly identical except that the skull in AMNH 55349 is less notched in the ear region behind the glenoid. The mastoid region, formed differently (see below), is slightly more squared in forming the back corner of the skull. These last two differences are considered independent of crushing in the fossil and represent valid distinctions in form. Unfor-

FIG. 2. AMNH 55349. *Vespertiliavus* cf. *bourguignati*. Stereophotographs of skull, dorsal view.

tunately, PU 11573 is poorly preserved in this area but does tend to be intermediate between AMNH 55349 and species of *Taphozous*.

Skull Face. The nasal opening in AMNH 55349, though not entirely clear of matrix (fig. 4), seems complete except for the premaxillaries, incisors, and a small part of the maxillary bone above the right canine. The nasal bones extend

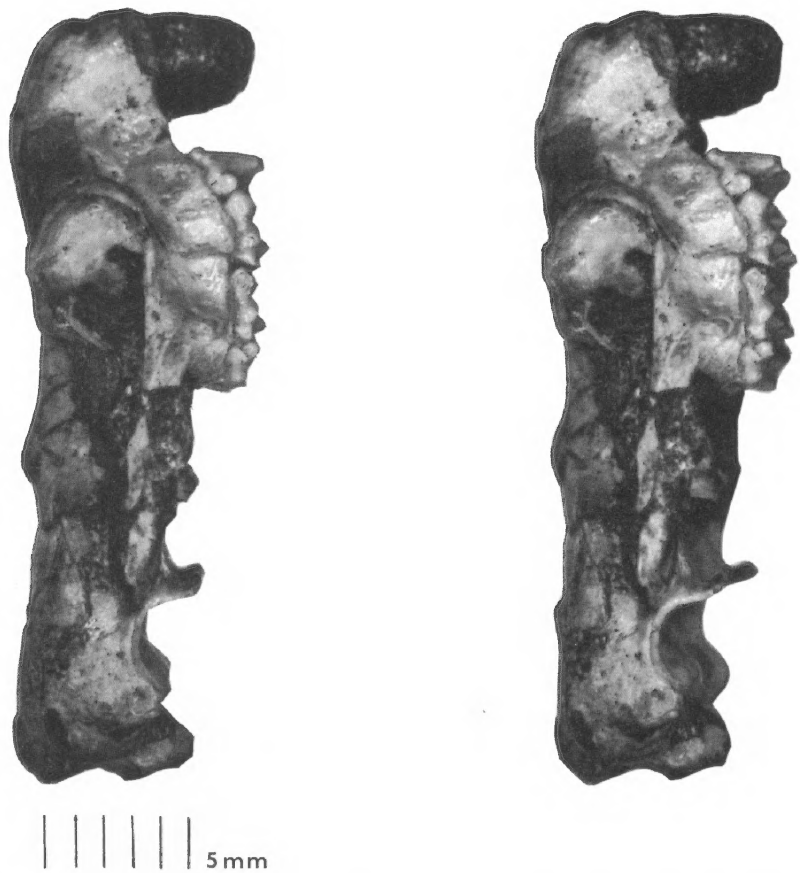

FIG. 3. AMNH 55349. *Vespertiliavus* cf. *bourguignati*. Stereophotographs of skull, lateral view.

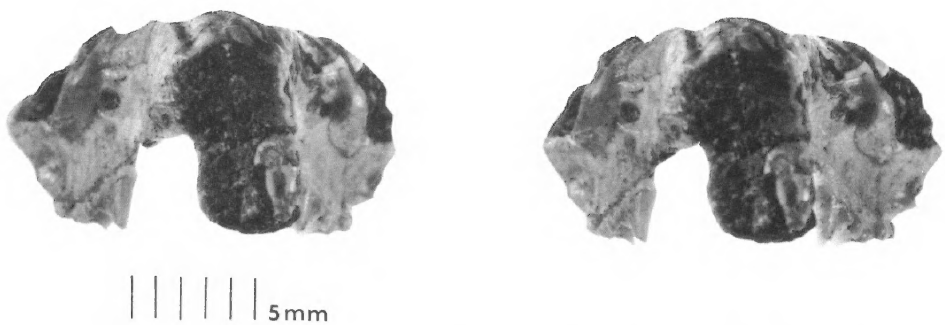

FIG. 4. AMNH 55349. *Vespertiliavus* cf. *bourguignati*. Stereophotographs of skull, anterior view.

FIG. 5. AMNH 55349. *Vespertiliavus* cf. *bourguignati*. Stereophotographs of skull, occipital plane.

far forward on the snout to a line over the front half of the canines. As a result the nasal opening lies in a nearly vertical plane, a condition accentuated by the curvature of this part of the snout. As in most modern specimens, sutures in this area cannot be made out and it is difficult to see from this material, or from his plates, the basis for Revilliod's (1920) description of the shape of the nasal bones. The angle of the nasal opening (exclusive of premaxillary bones) is oblique in emballonurids where it is not formed by deep notching of the snout and palate between the canines. The nasal grooves described by Revilliod (1920, p. 92) are prominent here and run straight forward from the so-called supraorbital foramina to the edge of the nasal opening (fig. 2). Here they are associated with a slight notching of the anterior border of the bone. The posterior part of the premaxillary bone in PU 11573 rests seemingly loosely on the maxillary beside this groove. The bone is flat at its posterior end, but becomes tubular anteriorly as it lines the sides of the nasal opening. The front tubular portion, which is hollow, is pointed medioventrally and extends about halfway to the midline of the narial opening as seen in direct anterior view. The single incisor takes root not out of the end of the premaxillary, but from the anteroventral side of the tubular portion. The tooth has a round neck, long, simple, conical form with some curvature, and is oriented slightly anterolaterally,[1] much as in *Rhinopoma*. It has roughly the diameter of P^1 to judge from the alveolus of the latter, and is about 3/4 mm.

[1]As disclosed during preparation; subsequently broken off at the neck, the incisor is preserved, although the break was not clean enough to enable exact replacement.

long. *Saccolaimus* resembles PU 11573 in having the premaxillaries widely and laterally placed as seen in anterior view. However, the incisors are reduced to small nubbins. *Taphozous* tends to resemble PU 11573 in having larger incisors, which are still recognizably long and conical. The posterior of the two upper incisors in *Emballonura* seems to indicate that the lateral one has been retained in *Vespertiliavus*, *Taphozous*, and *Saccolaimus*, whereas all other emballonurids have the medial one, rooted directly at the end of the tubular portion of the premaxillary. However, the situation in the smaller forms is not entirely clear, for the entire remaining structure, bone and tooth, is very reduced in many cases; the morphology may be homologous to that in the larger forms with additional loss of the medial alveolar structure. (The Diclidurinae, interestingly, have unique complex incisors, generally similar to the canines in cusp morphology.)

Nasal grooves are present in *Taphozous nudiventris* (but not in other species of the genus) as shorter, shallower depressions that nest the dorsal leaves of the premaxillary bones and extend but a short distance behind them. They end abruptly not in foramina, or if so the foramina are minute. The supraorbital foramina in AMNH 55349 are small, located immediately in front of the postorbital ridges (which join posteriorly to form the sagittal crest) and close to the posterior edge of the postorbital bars. The infraorbital foramen is large in both *Taphozous* and *Vespertiliavus* (fig. 4). In *Taphozous* it is actually the confluence of two to four openings from the nasal region dorso-anteriorly and from the orbit posteriorly. In various species of *Taphozous* observed one or more of these may open separately onto the surface; the condition

can even vary from side to side. The internal complexity has not been prepared out fully in the fossils, but in AMNH 55349 the left opening appears to be paired, the right single. In both the fossil and Recent genus the opening(s) is (are) always above P^{last}.

As in the nasal region sutures cannot be made out in the orbital region, and no defining statements on extents of bones are possible. The circumorbital rim appears very pronounced in AMNH 55349, more so than in *Taphozous* and *Saccolaimus*; this is considered not to be a matter of skull size. The maxillary bone over the roots of the cheek teeth is so thin as to barely cover them and the entire cheek area is deeply concave. In living bats this area marks the origin of the buccinator musculature, but in no other emballonurid, including the comparably sized *Saccolaimus*, is it quite so extensive or deeply excavated as in AMNH 55349. The postorbital bar is perhaps less slender than in *Taphozous*, but seems otherwise comparable in form.

The following foramina open into the orbitosphenoid region (includes here orbit proper, dorsal surface of maxillary over the teeth alveoli, palatine, orbitosphenoid, and alisphenoid bones). See also Pterygoid Region below. The lacrimal foramen opens into the lacrimal bone inside the orbit (that is, posterior to the circumorbital rim, fig. 6). In *Taphozous*, with nearly identical morphology, the canal from the lacrimal foramen passes close behind, above, and at right angles to, the infraorbital canal; only a thin wall of bone separates these in passing. In other emballonurids the lacrimal foramen opens in front of (or just on the edge of) the circumorbital rim. Opening into the orbit next ventrally and posteriorly to the lacrimal is the small sphenopalatine foramen, whose canal courses through to the internal nasal passage in an anterior direction. Just ventral and posterior to this the maxillary foramen marks the entrance of the infraorbital canal into the orbit. It may be larger or smaller than the sphenopalatine among microchiropterans generally; it is roughly the same size in most emballonurids, larger in *Taphozous*. Several alveolar foramina pierce the thin bone covering the molar roots in this region. Medially, on the dorsal surface of the posterior palatine border, the posterior palatine foramen leads quickly through to the palate. It is the fourth major foramen in the orbital region; it lies distinctly separate from the sphenopalatine and maxillary (contrast *Canis* in which this and the sphenopalatine are nearly confluent, but compare *Pteropus*, *Saccolaimus*, and *Didelphis*). Another foramen opens dorsally and somewhat medially to the posterior palatine; like the sphenopalatine it too leads into the nasal cavity. In *Taphozous* it is smaller than the sphenopalatine and posterior palatine, and is situated at the anterior end of the recess in the side of the skull resulting from relative expansion of the cranium. (*Pteropus* has similar additional openings from the orbital region to the nasal passages.)

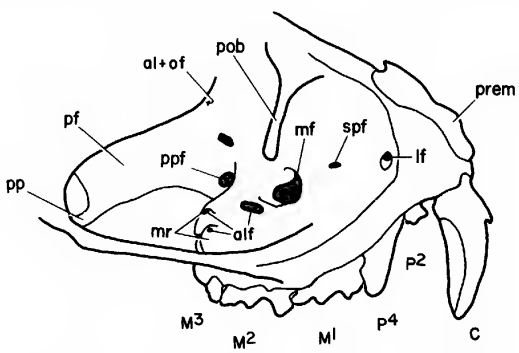

FIG. 6. Right orbital region of *Taphozous nudiventris*, AMNH (Mam) 27391, to show foramina discussed in text. View is lateral and slightly posterodorsal. Camera lucida drawing. Approx. ×4. Abbreviations, pp. 2-3.

Skull Roof. Condition of the dorsal cranium in AMNH 55349 (fig. 2) of course depends on reconstruction, but the following features are of interest. The sagittal crest was a low but distinct ridge not produced posteriorly as in *Saccolaimus*; it is closest to some species of *Taphozous*. The roofing bones give no indication that cranial inflations were present. PU 11573 differs markedly from AMNH 55349 in these features. Cranial inflations were well developed and apparently no sagittal crest was present. This condition is approached by some of the smaller species of *Taphozous*.

Both *Taphozous* and *Saccolaimus* exhibit a large foramen (possibly for the mandibular-alveolar vein) which communicates with the sinus in the postglenoid process and opens in the squamosal just dorsal to the glenoid surface and at a level anterior to the base of the zygo-

matic arch. No other chiropteran examined has this foramen so large and anteriorly placed. AMNH 55349 lacks any indication of such an opening. PU 11573 posesses two moderately sized foramina opening from the squamosal dorsal to the glenoid, but they are level with and posterior to the base of the zygomatic arch.

Palate. Preservation of the palate does not obscure the fact that it was long and arched dorsally between the tooth rows. The anterior border is not prepared in AMNH 55349; in PU 11573 the notching under the nasal opening comes back no farther than C. The posterior lateral border of the palate in AMNH 55349 (only), rather than skirting closely the neck of M^3 (compare *Taphozous* and *Saccolaimus*), passes straight medially to form a shelf behind the protocone of M^3 before curving to form a recess beside the pterygoid. Two small foramina open in the palate, one medial to the front edge of M^1, the other medial to the protocone of M^2. The posterior one is presumably the palatine; the anterior one an additional foramen from the nasal cavity. In PU 11573 both foramina are relatively larger.

Dentition. Formula: *1. 1. 3. 3.* All other emballonurids except *Emballonura*: *1. 1. 2. 3.* (figs. 1 and 7).

The right canine in AMNH 55349 is prepared only on the front and side. The left, broken off irregularly at the base, shows a slightly subdivided pulp cavity and a posteromedial thickening of dentine in section, indicating perhaps that the canines here, as in the rest of the family, had subsidiary posterior cusps. PU 11573 has the left canine fully preserved, broken off at its base and replaced; the right is missing except for the base of the crown. No posterior subsidiary cusp is indicated for either tooth. Only one other upper canine is figured for *Vespertiliavus* (Revilliod, 1920, p. 88, fig. 28). The diagram is unclear in its perspective, but it shows the tooth broken near the tip, the pulp cavity simple in cross section, and no posteromedial subsidiary cusp, only a cingulum. In the modern genera the subsidiary cusp is at the end of an internal cingulum, and in some of the smaller forms may be little more than a point on the crest as its skirts the posterior border of the tooth.

Vespertiliavus had three premolars: one small and single-rooted, one larger and double-rooted, and the last very large and triple-rooted. All premolars are present in the type of the type species and the same premolar count is indicated by all referred material. (Schlosser 1877, p. 72 incorrectly considered the middle premolar as single-rooted.) *Taphozous* and other living genera have retained P^1 and P^{last} (P^1 being the first of the premolar count primitive to bats, a moot point—see Miller, 1907, p. 24). P^{last} for all the family is molariform in being as high and nearly as wide as M^1 and in having a lingual shelf behind the protocone. In crown view the tooth is irregularly triangular in outline. The paracone is the dominant cusp, tallest in fact of all the upper cheek teeth cusps (worn apically in AMNH 55349). Its surface is convex, conical labially, flat to concave posterolingually, and continuous with the protocone basin. A posterolingual cingulum (terminology of Phillips, 1971, pp. 7-8) surrounds the basin and continues in a more or less

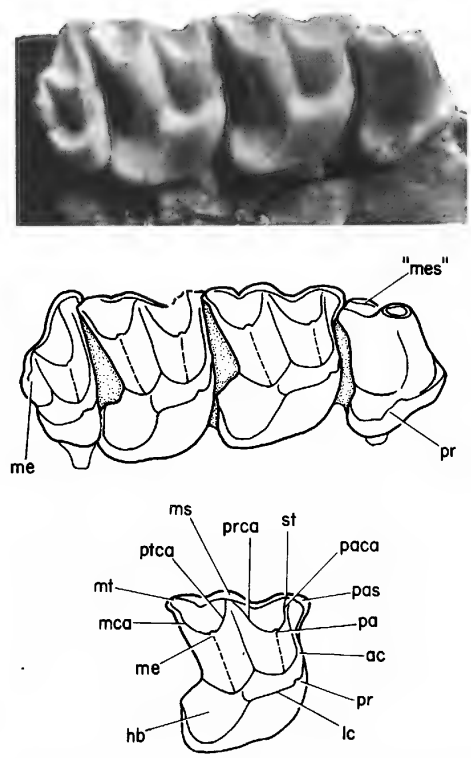

FIG. 7. Upper right dentition of AMNH 55349. *Vespertiliavus* cf. *bourguignati*, P^4-M^3. View is oblique: anterolabial and ventral. Approx. × 11. Stipple: matrix. Abbreviations, pp. 2-3.

straight course anterolabially until it curves around the front and close to the base of the paracone; it is not continuous on the labial side of the tooth. The protocone is a small cusp situated on the cingulum roughly at the level where the lingual slope of the paracone becomes convex. No anterior cingular style (cuspule of Phillips, 1971) is evident on the anterior cingulum. The only other distinctive cusp on P^{last} is what, for the sake of its position with respect to the paracone and for convenience, may be termed a "mesostyle." In form it is more a short cingulum on the posterolabial slope of the paracone (or more exactly, the precentrocrista). Anteriorly it reaches to the level of the base of the paracone proper; posteriorly it nearly touches M^1 parastylar area. PU 11573 differs in P^{last} morphology in the following: protocone better developed on lingual cingulum, with apex quite distinct; anterior cingular style slightly better developed, apex distinct; "mesostyle" less well developed. Among living genera the features described here are somewhat variable, but generally (1) protocone is distinct and convex lingually; (2) anterior cingular style is distinct, sometimes subequal to or even larger than the protocone in size, such that the two cuspules make the anterolingual outline of the tooth, as seen in crown view, bilobate instead of straight to apical; (3) "mesostyle" is less well developed, if at all; (4) precentrocrista slopes more sharply dorsally away from the apex of the paracone, and in some cases (*Saccopteryx bilineata*) a cusp is present at its posterior end, abutting M^1 (?a true mesostyle). In features (1) to (3) PU 11573 is closer to most of the modern forms than to AMNH 55349.

M^1 and M^2 are similar in morphology and nearly the same size (maximum crown dimensions, AMNH 55349, 2.5 by 2.5 mm.). Both are dilambdodont, strongly divided into a high labial surface consisting of two triangular subdivisions ("elements" of Phillips, 1971) formed of the paracone and metacone, and a lower lingual surface comprised of the protocone and hypoconal basins. The metacone is characteristically higher than the paracone (especially on M^1), nearly equal in height with the mesostyle. The ectoloph runs from an anterior parastyle through stylocone (terminology of Van Valen, 1966, p. 8) and (highest) mesostyle to metastyle, but is either worn off or not developed as a sharp ridge behind the mesostyle. The ectoloph in both fossil skulls at hand is developed such that it forms a fairly high labial border for both elements in each molar; in all living forms the surfaces of the elements are more deeply basined and the ectoloph on their labial sides more deeply notched. In the fossils an anterior cingulum present on *both* molars, but particularly on M^2, connects the stylocone to protocone. Precentrocrista and postcentrocrista do not intersect each other, rather they join the mesostyle separately (probably a consequence of wear). The protocone is at the junction of the anterior and lingual cingula. Where these crests do not affect its form it can be seen that the cusp is conical in shape. Seen in direct lingual view, its apex forms the highest point of the inner edge of each of M^1 and M^2 (not entirely evident from fig. 6 due to perspective). Posterior to the protocone the lingual cingulum (not postprotocrista of Phillips, 1971, p. 8; see below) deflects sharply dorsally (as seen in direct lingual view) and lingually (as seen in direct crown view) at a level somewhat anterior to the base of the metacone. The point of this deflection has no established name. Homology with a metaconule seems unconvincing because (1) the crest posterior to this point is the internal cingulum continuing to the hypocone, not to any part of the metacone; (2) the morphology in question is neither crescentic nor connate—not a distinct cusp; (3) in some of the modern forms (e.g., *Saccopteryx*) the postprotocrista running from the base of the metacone is distinct and does not involve this part of the tooth.

Labial to the protocone, the lower shelf of the molars consists of the protocone basin that extends between the paracone and metacone. Its surface is simple except for the slight convexity of the posterolabial slope of the protocone. Posteriorly the surface of the tooth deflects dorsally to form the hypoconal basin; thus the boundary between the basins is only roughly homologous with the postprotocrista. In AMNH 55349 this boundary is a smooth convexity in M^1 and M^2; in PU 11573 it is a smooth convexity in M^1 and more a sharp crest in M^2. In some *Taphozous* species it is similar to AMNH 55349. In other species and in *Saccolaimus* it is barely discernible

at all; here the two basins together form a simple posterodorsally sloping surface. Among the smaller emballonurids most genera have some expression of a true postprotocrista running directly from the base of the metacone toward the protocone, and thus dividing the two deeply excavated basins. This is considered to be a primitive character (see also Slaughter, 1970, p. 64). In some genera (*Chilonycteris*, *Furipterus*, *Mormoops*, *Mystacina*) where the hypocone is developed as in emballonurids, the postprotocrista is also preserved. Diclidurines have a smoother convexity dividing the basins as in AMNH 55349. Among other genera *Cormura brevirostris* is closest to *Saccolaimus* in this feature.

The hypocone has two distinct and recognizable forms in emballonurids. In the smaller genera it forms a distinct cusp on the posterolingual cingulum, always medial to the base of the metacone, that is, on a level anterior (as seen in direct lingual view) to most of the hypoconal basin. *Taphozous*, *Saccolaimus*, and *Vespertiliavus* are interpreted as having lost the distinctive apex of the hypocone. In these forms the hypoconal basin is rimmed by an even cingulum (PU 11573 shows a deflection in the course of the cingulum but no well-defined cuspule).

One difference between M^1 and M^2 is the relative extent of the parastylar area. In both teeth the parastyle when fully present abuts the preceding tooth and is situated on a level in front of the anterior cingulum (as seen in direct lingual view), whereas the stylocone is connected to the parastyle by a short curved portion of the ectoloph and is higher than the paracrista. Parastyle and stylocone are strongly convex labially and even ventrolabially. In *Vespertiliavus* M^1 relative to M^2 has a lower parastyle and stylocone relative to the surrounding crown and a narrower anterior cingulum along the paracrista face. In *Taphozous* a complete anterior cingulum on M^1 has been lost; it runs into the face of the paracrista from the parastyle. In some species the same is true of M^2. In *Saccolaimus* the complete anterior cingulum has been lost on both M^1 and M^2, and the ectoloph does not connect smoothly the parastyle and stylocone but is notched between them. In all the smaller genera the parastylar area is greatly reduced in M^1. In some cases the parastylar area is lost and the tooth is surrounded merely by a continuation of the low lingual cingulum (see table 2).

M^3 in *Vespertiliavus* is roughly half as long as M^1 and M^2 and, at its widest extent between parastylar area and protocone, is equally as wide as these teeth. The ectoloph, in crown view, runs in an extended S-shaped course from parastyle through stylocone before joining the mesostyle. Throughout its course it is a distinctive crest with a strongly convex labial surface, as is the anterior ectoloph on M^1 and M^2. Parastyle and stylocone cusps are as separated from each other as in M^1 and M^2; the highest part of the ectoloph runs between them. The anterior cingulum on M^3 is complete. The protocone is distinct but not as well developed as on M^1 and M^2. Anterior and posterior lingual cingula curve symmetrically from the protocone (as seen in direct crown view); the posterior one leads no farther than to the base of the metacone. The posterior slope of the tooth crown is formed by two convex surfaces, the mesostyle and the metacone. The mesostyle is relatively smaller and lower on the ectoloph than in M^1 and M^2; the metacone (as seen in direct lingual view) is lower than the paracone, unlike M^1 and M^2. The lengths of the crests bordering the elements are, in sharply decreasing order: paracrista, precentrocrista, and postcentrocrista.

Characteristically *Taphozous* and *Saccolaimus* have lost the metacone on M^3. The ectoloph is as in M^1 and M^2 deeply notched in the labial border of the remaining single element in these forms. The stylocone is the highest point on the tooth crown, the parastyle having been reduced. The anterior cingulum is not continuous about the base of the paracone; as seen in direct lingual view, it runs down from the parastyle into the base of the paracrista, at about the level of the base of the apex of the protocone. No distinct anterior or posterior lingual cingula flank the paracone. The cusp has a simple, medially canted, conical form, and is situated closer to the base of the paracone than in *Vespertiliavus*. The development of a protocone basin is variable in *Taphozous* species but everywhere much less than in *Vespertiliavus*. All the smaller emballonurids have a metacone on M^3, although as in *Vespertiliavus* the tooth is not fully dilamb-

dodont. Ectoloph, parastylar area, anterior cingulum, protocone, and posterolingual cingulum are generally as in the fossil forms, except: the anterior cingulum may be more pronounced and the ectoloph more deeply notched as in all the modern anterior molars. The principal difference lies in the robustness of the metacone which is always strongly conical (except for the postcentrocrista) and higher than the paracone. In addition the protocone basin medial to the base of the metacone is more fully developed than in the larger living forms. Variably there is a very faint preprotocrista running lingually or even anterolingually toward the protocone.

Pterygoid Region. The only suture visible in the pterygoid region in AMNH 55349 is that between the palatine and pterygoid bones on the pterygoid flanges (fig. 1). The region otherwise consists presumably of vomer, posterior palatine, presphenoid, ventral frontal, alisphenoid, and anterior basisphenoid. The glenoid surface of the squamosal may also be considered here. The anterior side walls of the braincase (ventral facing surfaces of the frontal and alisphenoid) must be reconstructed from their configuration in PU 11573 and living forms. (The skull of *V. bourguignati* figured by Revilliod, 1920, plate I, fig. 13, shows mostly matrix in this region.)

The internal nares are separated by a septum of the vomer as they enter the mouth cavity. This septum itself is perforated by a canal which leads anteriorly to the nasal cavity (fig. 8A). Posteriorly the canal continues as faint, parallel grooves in a single trough in the presphenoid and basisphenoid as far back as the median border of the basisphenal pits. This trough is variously developed in species of *Taphozous*, *Saccolaimus*, and other emballonurids (fig. 8B, C), but never so broadly as in AMNH 55349. In *Taphozous* and *Saccolaimus* it is pinched laterally by slight inflations of the pterygoid and basisphenoid bones and issues from a minuscule opening in the vomer. In the shorter faced genera the canal opens more posteriorly between the pterygoid flanges in the basisphenoid area and may be hypertrophied in some cases (table 2).

The pterygoid flanges are simple; pterygoid processes may have been present, but have been broken off. The posterior edges of the pterygoid flanges curve down, back, and laterally to form

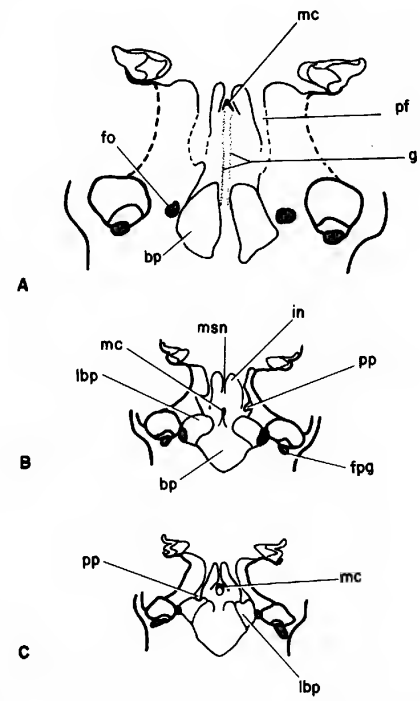

FIG. 8. Basicranial region of three emballonurid bats to show different states of character 4, table 2; see text. A. *Vespertiliavus* cf. *bourguignati*, AMNH 55349. B. *Peronymus leucoptera*, AMNH (Mam) 94474. C. *Balantiopteryx plicata*, AMNH (Mam) 208865. Ventral views. Camera lucida drawings, all approx. ×3. Abbreviations, pp. 2-3.

the anterior lateral edge of the basisphenal pits.

In bats generally the side wall of the skull is pinched in between the pterygoid flanges and the cranium. This feature is strongly developed in *Saccolaimus*, where (anteriorly) the optic plus anterior lacerate foramina and (posteriorly) the sphenorbital fissure plus foramen rotundum open downward from the braincase. In *Taphozous*, characteristic of the family, these two openings are separated by a strut of the orbitosphenoid bone, which sends a flattened, sliver-like process projecting forward over the anterior opening. In *Saccolaimus* these openings are widely separated and the recess between the pterygoids and braincase extends backward and medially to form a pocket behind the sphenorbital fissure. In AMNH 55349 this recess cannot be recon-

structed with much confidence, but it appears from the position of the alisphenoid bone in front of the foramen ovale that no pocket was developed here, rather that the recess was closer in form to *Taphozous*. PU 11573 also appears to be closer to *Taphozous*.

The zygomatic arch is straight as in the Emballonuridae and many genera outside the family. It ends beside the prominent glenoid surface which is concave, nearly as long as wide, and set dorsal to the most dorsal surfaces of the tooth crowns. In *Taphozous* and *Saccolaimus* the glenoid surface extends laterally to include the back part of the zygomatic arch, making the whole articulating surface a distinctly crosswise feature. In *Vespertiliavus* the surface ends medial to the zygomatic process of the squamosal. Backward movement of the condyle was prevented by the very prominent postglenoid process. This is about half as wide as the glenoid surface, its anterior face part of the articulating surface, and is therefore concave forward. The large postglenoid foramen opens vertically on its steeply sloping back side, giving the opening an elliptical shape. A small foramen opens on the lateral side of the postglenoid process at its junction with the zygomatic process of the squamosal only in some species of *Taphozous* and in *Saccolaimus*. The glenoid surface in AMNH 55349 is set on a prominent, heavy development of the squamosal in this region. Below the articulating surface the bone slopes convexly away to contribute together with the alisphenoid in front to the side wall of the cranium and posteriorly to the middle ear cavity (especially epitympanic recess). The foramen ovale opens in the alisphenoid on the side of this prominence and the course of the mandibular branch of V close against the bone is marked by a short vertical groove exactly medial to the glenoid surface. The alisphenoid extends posteromedially to touch the petrosal and form the posterolateral wall of the basisphenal pit. Cracking and subsequent infilling by calcite give the impression of sutures in the area. On both sides of the skull cracks pass through or just beside the foramen ovale and might be misinterpreted as sutures between the alisphenoid and basisphenoid, but the cracks are not symmetrical on the right and left sides. The same sort of cracking has separated the deeper walls of the basisphenal pits from the alisphenoid where it reaches the petrosal; this, too, is not an alisphenoid-basisphenoid suture.

Basicranial Region. The basicranial region is largely excavated by the basisphenal pits. These extend forward to the base of the pterygoid flanges, lateral almost to the foramen ovale, and posteriorly so far as to contour the front of the cochlea. The median septum of the basisphenoid is of some width all along its length, with the ventral surface flat and square-edged. The bone broadens posteriorly to form the floor of the skull between and behind the petrosals. Depressions in the basicranial region are present in several microchiropteran genera outside the Emballonuridae (see p. 21) with a distribution widely scattered and infrequent enough to suggest that outside this family they are not always homologous. The function(s) of the pits is (are) unclear. The feature is variable within the family, being least developed in *Emballonura sulcata* (but strongly developed in other species of that same genus), paired in some genera, unpaired in others (see p. 26). Its development does not seem to vary allometrically; pits are large dominating features in small-skulled forms (e.g., *Peropteryx*, *Peronymus*). In the size series *Taphozous melanopogon*, *T. nudiventris*, *Vespertiliavus* cf. *bourguignati*, *Saccolaimus peli*, they are nearly the same size throughout, despite a 25 percent range in skull length.

In AMNH 55349 the basioccipital medial to the petrosal is contoured such that it does not overlap the latter directly but forms a groove bordering it that runs back as far as the condyloid fossa. Near its anterior end this groove is interrupted by an extension of the petrosal, a thin lamina drawn in curved form from the otherwise smooth surface of the cochlea and articulating with the basisphenoid (fig. 9). The petrosal is thus anchored at the back walls of the basisphenal pits, posteromedially against the basioccipital, and medially at the lamina extension of the petrosal. If it can be inferred from the remaining morphology of this region of the basicranium that *Vespertiliavus*, like *Taphozous* and *Saccolaimus*, possessed a medial entocarotid (see below), then the artery should have entered the cranium just posterior to the meeting of the cochlear process of the basisphenoid and the lam-

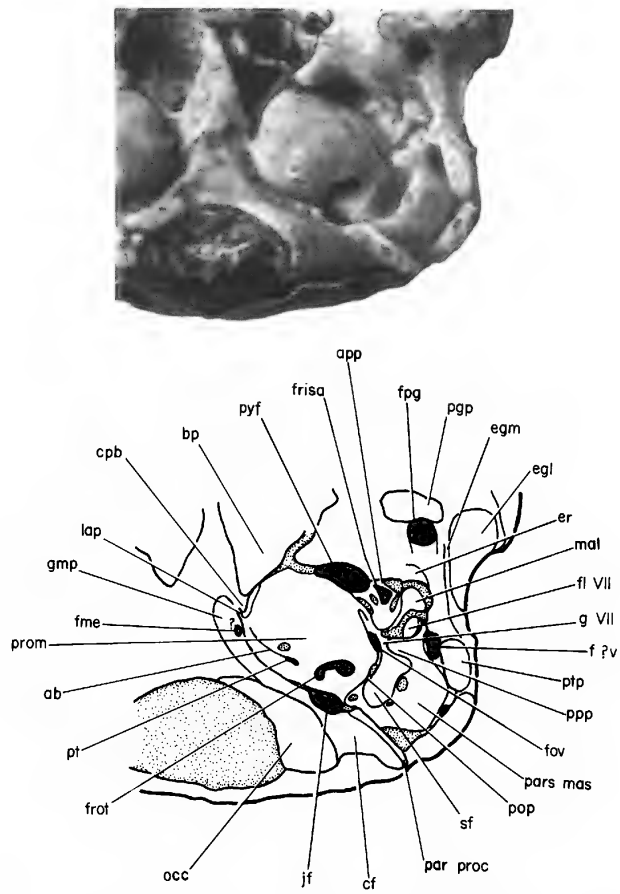

FIG. 9. Left ear region of AMNH 55349. *Vespertiliavus* cf. *bourguignati.* View is ventral and slightly posterior. Approx. ×8. Stipple: matrix. Abbreviations, pp. 2-3.

ina extension of the petrosal. Although matrix obscures the details, there appears to be space between the bones at this point for such an opening, though not so foraminate in form as in the two Recent genera. (PU 11573 has been distorted in this region.) The large hypoglossal foramen faces directly anteriorly into the groove about the petrosal (not visible in ventral view). The foramen magnum is excavated deeply into the posterior margin of the basioccipital, such that it opens ventroposteriorly from the skull. The articulating surface of the condyle is likewise directed downward and backward and is not a symmetrical knob, rather a curved linear feature.

In *Taphozous* and PU 11573 the basicranial bones are not quite so deeply grooved about the petrosals, but *T. nudiventris* approaches the condition seen in AMNH 55349. No lamina extension of the petrosal is present, and the cochlear process of the basisphenoid is present only as the border of an emargination of that bone. The medial entocarotid artery, having passed along the groove about the petrosal, presumably (in *Taphozous* at least) enters the cranium through this emargination. In *Saccolaimus* the situation is different. The basisphenoid anterior to the cochlear process extends up over the promontorium and is appressed to the fully ossified entotympanic in a vertically projecting knobby prominence (see p. 26). Between this and the entrance point of the medial entocarotid the border of the basisphenoid wraps down and medially about the basal turn of the cochlea.

Ear Region. AMNH 55349 has one of the best

preserved (and prepared) ear regions known for *Vespertiliavus* (fig. 9). The bulla and ossicles are, however, missing or present only as displaced fragments. The bulla in chiropters is nearly always attached so loosely to the skull as to leave little sign of its presence after removal. The skull is generally very thin in the region of the ectotympanic groove—no thicker, in fact, than the roofing bone (squamosal) that bounds the groove. Only in *Saccolaimus* and *Vespertiliavus* (AMNH 55349 more so than PU 11573, apart from pteropids, whose morphology is otherwise different) is this area widened to give the impression of an ectotympanic groove lateral to the posttympanic process. If the ectotympanic bone is comparably placed in *Saccolaimus* and the fossil genus, however, this external groove is not the line of its attachment: in the Recent form the ectotympanic rests medially to this line on a surface of the squamosal just behind the postglenoid foramen. Such a possible true area of attachment can be made out in *Vespertiliavus* as well (fig. 9, egm). The more lateral groove may have served in the attachment of the external ear. *Taphozous* approximates most other genera in lacking this morphology; here the dorsal part of the ectotympanic ring is flush with the thin side of the temporal skull.

The relations of the pars cochlearis to the bones surrounding the middle ear, particularly the alisphenoid, are not everywhere clear; but the morphology is certainly, as might be expected, close to that of *Taphozous*. The anterior part of the middle ear cavity remains unossified as the pyriform fenestra. This is a fairly restricted opening between the cochlea and the alisphenoid directly medial to the epitympanic recess. Exactly how the anterior process of the petrosal (terminology of Henson, 1970) meets the alisphenoid laterally to the pyriform fenestra is not clear in AMNH 55349, but it probably abuts closely. In *Taphozous* the anterior process of the petrosal is long and slender and projects anteroventrally from that bone (as seen in ventral view). Near its base (whether medial or posterior varies among species) is a foramen, probably for the ramus superior of the stapedial artery if this does not enter the cranium through the pyriform fenestra. This opening in the petrosal bone is not apparent in a selection of specimens of other chiropteran genera besides *Taphozous* and *Vespertiliavus* (not observable in *Saccolaimus* without dissection of the skull). The fairly broad groove for the facial nerve separates this opening from the base of the cochlea. The foramen for VII opens laterally from the side of the promontorium (opening not visible in ventral view).

As far as can be discerned in PU 11573 the anterior process of the petrosal is also slender and elongate as in *Taphozous*. It appears on this specimen to be medial to the arterial foramen. In AMNH 55349 the base of the process is evident just lateral to the arterial foramen. The process has been broken off in preparation, but the cross section of the base indicates that it was more flangelike than round, and probably lay more or less flat dorsoventrally against the alisphenoid bone. In general the epitympanic recess and this entire part of the tympanic cavity are relatively deeper in AMNH 55349 than in other specimens observed. Both skulls of *Vespertiliavus* show narrower epitympanic recesses than in species of *Taphozous* (*Saccolaimus*: not visible without dissection).

Behind the anterior process the lateral edge of the petrosal bone curves backward and dorsally and is appressed closely to the squamosal in AMNH 55349. Part of its edge forms a medially directed flange that completes the facial canal and forms the medial wall of the epitympanic recess. Following backward, this lateral edge terminates in the prominent posterior process of the petrosal that overhangs the stapedial fossa and nearly touches the promontorium. The groove for VII is a broad shallow excavation about the base of the promontorium leading into the stapedial fossa. The fenestra ovalis opens out over this groove. It is separated from the slightly larger fenestra rotundum by a small prominence on the promontorium. In *Taphozous* the homologous structure is a ridge of bone that actually projects over the stapedial fossa (Segall, 1974); *Saccolaimus* is closer to *Vespertiliavus* in lacking this structure. In *Taphozous* the internal carotid artery enters the middle ear just lateral to the tubercle (see below), in a gap between the entotympanic and petrosal. A slight groove for the artery is barely imprinted on the promontorium just above the fenestra rotundum in both this genus and the fossils. Above and medial to

the fenestra rotundum is a small tubercle on the promontory surface which is perforated at its tip. This terminates the curved lamina, present particularly on AMNH 55349, which runs to the cochlear process of the basisphenoid. In specmens of *Taphozous*, which have nearly identical morphology, the posteromedial corner of the entotympanic rests on this tubercle and in some specimens vessels or nerves can be seen entering its opening. The unossified portion of the entotympanic fastens to the petrosal along the lamina.

PU 11573 has part of the right bulla preserved. According to the criteria of van Kampen (1905, pp. 458-459; see also van der Klaauw, 1931, pp. 268-269), the portion consists of the ectotympanic and parts of the entotympanic. (Henson, 1961, p. 157, and fig. 1, however, refers to comparable structures as ectotympanic only.) The anterior and posterior legs (terminology of Henson, 1961) of the ectotympanic nearly meet, as in *Taphozous*. Only part of the medial edge of the entotympanic is preserved in the fossil, but to judge from the molding on the associated matrix, the bulla in this specimen was narrow anteriorly, without stylar process of the tympanic as in *Taphozous nudiventris*, and broader posteriorly. It was not so expanded as in other large emballonurids, but closer perhaps to the condition seen in some of the smaller forms (*Cormura*, *Diclidurus*, *Saccopteryx*). Although the promontorium of PU 11573 shows the tubercle described above, there is no ridge extending forward from it. It is possible that the bulla of AMNH 55349 would be broader and ossified more extensively than that shown by PU 11573. Van Kampen (1905, p. 459) cited a remark by Otto (1826) that the bulla in bats becomes more ossified with age.

In *Saccolaimus* there is no tubercle and ridge on the promontorium, the basisphenoid rather overlaps the cochlea as described on p. 16. The medial edge of the entotympanic is draped over this topography, tightly enclosing the middle ear cavity. Such a fully ossified bulla (seen in all specimens of *Saccolaimus* examined) is very rare among bats, noted also by van Kampen (1905) only for *Plecotus auritus*.

The pars mastoideus of the petrosal in AMNH 55349 consists of the posterior process of the petrosal, the stapedial fossa, and a broad, posteroventrally facing area behind the fossa that constitutes the surface expression of the semicircular canals within the bone. The mastoid petrosal has become slightly separated from the squamosal bone and seemingly rotated forward relative to it, although the relations with the rest of the squamosal indicate that the latter has been displaced. A moderate-sized foramen opens between these two bones just lateral to the posterior process (fig. 9, f?v); the opening is round anteriorly and tapers to a slit posteriorly, medial to the posttympanic process. The course of the exiting vein (presumably) is marked by complementary grooves in the mastoid and squamosal. No such foramen is present in *Taphozous* at the same point, but there is a possibly homologous opening between the two bones behind the posterior process. However, it is difficult to assess the size or significance of this opening since in this genus it is situated between bones that are not closely appressed, and possible post mortem distortion in the Recent specimens examined makes its original form unclear. In *Saccolaimus* the mastoid and squamosal are sutured in this area; the mastoid is contoured around a medially directed prominence of the squamosal at the base of the posttympanic process, such that the entire joint is tightly structured. There is apparently a very small foramen in this suture at the base of the posttympanic process; that this is homologous to the much larger opening in AMNH 55349 is questionable. The posttympanic process is long anteroposteriorly and heavy in AMNH 55349, *Saccolaimus*, and *Taphozous nudiventris*; smaller and thinner in *T. melanopogon* and the smaller emballonurids. The jugular foramen is proportionally larger in *Taphozous*, in which the delimiting bones are loosely associated in this area, small in *Vespertiliavus* and *Saccolaimus*, but of the same morphology in all.

In *Taphozous* the bony ridge overhanging the stapedial fossa (p. 17, and fig. 9, pop) is continued posteromedially in a ridge which projects ventrally in the face of the fenestra rotundum. The membranous portion of the bulla stretches behind the fenestra rotundum and attaches here. In *Vespertiliavus* and *Saccolaimus* this feature is present as a lower prominence of the pars mastoideus, a posteromedial termination of the

stapedial fossa. The ossified bulla in *Saccolaimus*, however, attaches not to the prominence, but rather to part of the paroccipital process medially. The mastoid is notched medial to the prominence; a short canal thus runs under the posterior edge of the entotympanic bone where it is anchored on the paroccipital, and leads over the jugular foramen.[1] In AMNH 55349 the prominence on the mastoid and the base of the paroccipital process are separated by a matrix-filled space. Since the petrosal may have settled relative to the squamosal bone, there is no strong argument to identify this with the morphology found in *Saccolaimus*. It appears to be another indication that *Vespertiliavus* lacked a fully ossified bulla, that found in *Saccolaimus* being a unique derived feature.

The epitympanic recess in AMNH 55349 is formed much as in *Taphozous* but is less deeply excavated laterally into the squamosal. The malleus (partly damaged) lies with its head, neck, and anterior process in the recess and its manubrium stretching across the facial canal toward the fenestra ovalis. The malleus had a well-developed spherical orbicular apophysis (terminology of Henson, 1961), detached but preserved in the course of preparation. The muscular process for attachment of the tensor tympani has been broken off, and the manubrium is also slightly damaged at the tip. The malleus appears closer to that of *Taphozous* than *Saccolaimus* in the possession of a well-developed orbicular apophysis. No other ossicles are recognizable in the specimen as currently prepared.

Occipital Region. The occipital region in AMNH 55349 is formed by the occipital, squamosal, and mastoid petrosal bones (fig. 5). The lambdoid crest is a low but distinct edge running from one posttympanic process to the other. The occipital condyle is more robust than in either Recent genus. It is flanked by a deep ventral condyloid fossa. The paroccipital process lateral to this is a delicate but well-developed flange of bone with its back surface facing posteroventromedially; it forms the lateralmost part of the exoccipital bone and articulates on its front base with the mastoid petrosal and squamosal bones. The posterior roofing of the skull is thus deeply notched between the paroccipital process and the posttympanic process of the squamosal, and the notch is filled by the mastoid petrosal containing the semicircular canals. The supramastoid foramen opens dorsal to the ventral condyloid fossa, about midway on the occipital surface. The same is true for *Taphozous*, but *Saccolaimus* appears to lack this opening. In *Saccolaimus* the nuchal and parietal crests are drawn into a posteriorly directed point, whereas in AMNH 55349 the nuchal line continues smoothly over the top of the skull. Both forms differ from *Taphozous*, in which the foramen magnum is relatively larger (in relation to occipital area) and the occipital surface, as also in PU 11573, is more domed to reflect this larger size and the more highly arched cranium.

[1]The function of this canal in *Saccolaimus* is unclear; perhaps it houses the internal carotid artery if this does not pass medial to the paroccipital process. The branching of the medial entocarotid from the internal carotid presumably occurs anterior to this canal, since the internal carotid presumably enters the middle ear in all three genera at a point on the promontorium anterior to the jugular foramen.

NOTES ON CHARACTERS AND HOMOLOGIES USED IN HYPOTHESIZING RELATIONSHIPS AMONG EMBALLONURID GENERA

This section discusses the characters listed in table 2 and notes briefly the distribution of some of them outside the Emballonuridae in cases where this distribution appears pertinent to understanding the primitive or derived condition within the family. The outgroup comparison, cursory and by no means comprehensive, has been based on a selection of genera that are themselves not grouped here into any preferred arrangement but merely listed to show how widespread certain characters may be. The survey is based on examination of specimens in the collections of the Department of Mammalogy, AMNH, except for the following, where the literature was consulted: *Cyttarops* and *Depanycteris* (Thomas, 1913, 1920), *Craseonycteris* (Hill, 1974), †*Palaeophyllophora* and †*Pseudorhinolophus* (Revilliod, 1920), *Boneia*, *Hipposideros*, *Pteronotus*, and *Glossophaga* (Miller, 1907), and *Cardioderma* (Koopman, personal commun.). Morphological description is presented to the ex-

TABLE 2

Character Distribution Chart for Genera of Emballonurid Bats
(Unless otherwise noted: – character absent; + character present.
For interpretation of primitive and derived conditions see text.)

Operating Taxonomic Unit (OTU)	† *Vespertiliavus*	*Taphozous*	*Saccolaimus*	*Emballonura*	*Cormura*	*Centronycteris*	*Saccopteryx*	Diclidurinae	*Peropteryx*	*Coleura*	*Peronymus*	*Balantiopteryx*
1. Reduced premaxillaries	+	+	+	+	+	+	+	+	+	+	+	+
2. Basisphenal pits	2	2	2	1/2	2	2	2	2	1	1	1	1
3. Lateral basal pits	–	–	–	+/–	–	–	–	–	+	+	+	+
4. Canal and grooves in interpterygoid region	++	+	+	+	+	+	+	–	+	+	+	+
5. Nasal inflations	–	–	–	+	+	+	+	–	+	+	+	+
6. Nasal depression	–	+	–	+	–	–	–	++	–	–	–	–
7. Postorbital bar	+	+	+	+	+	+	+	+	+	+	+	+
8. Supraorbital foramen	+	–	+	–	–	–	–	+/–	–	–	–	–
9. Position of lacrimal foramen (– out; + in)	+	+	–	–	–	–	–	+	+	–	+/–	–
10. Length of snout (– short; + long)	++	+	–	–	–	–	–	–	–	–	–	–
11. Pterygoid region length (– short; + long)	+	+	+	–	–	–	–	–	–	–	–	–
12. Inflated cranium	+/–	+/–	–	+	–	–	+/–	+	+/–	+/–	–	–
13. Inflation and exposure of semicircular canals	–	+/–	–	+	+	+	+	+	+	+	+	+
14. Upper incisor count	1	1	1	2	1	1	1	1	1	1	1	1
15. Upper premolar count	3	2	2	2	2	2	2	2	2	2	2	2
16. panterior (– short; + elongate)	–	+/–	+	–	–	–	–	–	–	–	–	–
17. Hypocone distinct	–	–	–	+	+	+	+	+	+	+	+	+
18. Parastylar area on M^1 (+ fully developed; – reduced or absent)	+	+	+	–	–	–	–	–	–	–	–	–
19. Anterior cingulum on M^1 (+ complete; – absent)	+	+/–	–	+	+	+	+	+	+	+	+	+
20. Metacone on M^3	+	–	–	+	+	+	+	+	+	+	+	+

TABLE 2 – (*Continued*)

Operating Taxonomic Unit (OTU)	†*Vespertiliavus*	*Taphozous*	*Saccolaimus*	*Emballonura*	*Cormura*	*Centronycteris*	*Saccopteryx*	Diclidurinae	*Peropteryx*	*Coleura*	*Peronymus*	*Balantiopteryx*
21. Reflected ascending ramus and angle of jaw (– slightly reflected; + strongly reflected)	–	–	–	+	+	+	+	+	+	+	+	+
22. Lower incisor count	3	2	2	3	3	3	3	3	3	3	3	3
23. Separate opening by foramen ovale	–	–	–	+	–	+	+	+	+	–	+/–	–

tent needed to distinguish primitive from derived conditions, or otherwise to indicate the variation which is encountered within the family.

1. Reduced premaxillaries: In all emballonurids the premaxillaries are reduced to bony splints which characteristically (1) do not contribute to the anterior surface of the palate (as in *Rhinolophus*, *Pteropus*, *Artibeus*, etc.); (2) never meet medially; and (3) rim the sides of the external nares in a loose association (not tight suture) with the maxillary bones. The upper incisor(s) is (are) essentially vestigial. This combination of premaxillary characteristics appears to be restricted to the Emballonuridae. Similar premaxillary morphology is found in the genera *Tadarida*, *Lasiurus*, and *Eptesicus*, but in all the premaxillaries are fused to the maxillaries, and the incisor(s) (is) are more prominent.

2. Basisphenal pits: These are characteristically developed in emballonurids, but basicranial depressions also occur in: *Nycteris*, *Mormoops*, *Phyllostomus*, *Tadarida*. In *Lavia*, *Desmodus*, *Lasiurus*, *Myotis*, and several other genera, possibly homologous structures are barely discernible; the condition in emballonurids appears to be the hypertrophy of a widespread feature. Depressions more anteriorly situated are found in *Rhinolophus* (median), *Natalus*, and *Thyroptera* (paired). In the larger emballonurids the ventral plane outline of the pits takes roughly the form of a bisected diamond; in the smaller emballonurids the form is more of a bisected circle (but not consistently so–e.g., species of *Emballonura*). As noted on p. 15 this difference may result from difference in skull size without concomitant difference in pit size.

3. Lateral basal pits (= pterygoid pits of Sanborn, 1937): These develop associated with the median basisphenal pit, separated from it by partial bony septa, and bordered anteriorly by the pterygoid flanges. They vary in extent of development from barely discernible (*Emballonura alecto*) to major depressions involving lateral bulging of the pterygoid flanges.

4. Canal and grooves in interpterygoid region: See p. 14 for morphology in *Vespertiliavus* and related genera. Canals in the internasal septum of the vomer occur in: *Chilonycteris*, *Micronycteris*, *Eptesicus*, *Myotis*, *Pizonyx*, *Mystacina*, †*Palaeophyllophora*, and other genera. Their size varies and they may or may not be associated with grooves in the presphenoid and basisphenoid. The canal in the vomer is relatively small where found in emballonurids in comparison with most of these genera. In *Peronymus* and *Balantiopteryx* the canal opens more posteriorly between the pterygoid flanges rather than at or anterior to the internal nares. The canal is paired in *Balantiopteryx* and the associated groove is more a wide, local depression in the basisphenoid.

5. Nasal inflations: Characteristically in the

smaller emballonurids the nasal and maxillary bones are inflated and thinly ossified on the sides of the snout between the orbits. Generally the inflation leaves the snout laterally expanded and dorsally flat (except *Emballonura* in which the median area has a furrowed form, and *Balantiopteryx io* in which the inflations are two spaced hemispherical protuberances on the anterior part of the snout as in *Rhinopoma* and *Craseonycteris*). Nasal inflations, of various form, also occur in: *Rhinolophus*, †*Pseudorhinolophus*, *Mormoops*, and possibly *Lasiurus*.

6. Nasal depression: In most emballonurids the surface of the skull is somewhat concave anterior to the bifurcation of the sagittal crest. In *Taphozous* (some species more than others) and *Peropteryx* this feature is accentuated to give a medial depression between the postorbital bars. In diclidurines the skull anterior to the sagittal crest is inflated (convex) on this primitive pattern, and, additionally, lateral nasal depressions are developed in the maxillary bone near the postorbital bar. Nasal depressions are also encountered in: *Lavia*, *Nycteris*, *Rhinopoma* (compare *Taphozous nudiventris* primitive pattern), *Craseonycteris*, *Rhinolophus*.

7. Postorbital bar: The relative length of the postorbital bar varies somewhat in the Emballonuridae but the structure is always present. Also present in: Pteropidae, *Nycteris*, *Lavia*, *Cardioderma*. Weber (1927, p. 133) argued that the postorbital bar develops in connection with a more powerful bite, seeming to imply that it is independently derived in those forms which have it. The functional significance of the bar is not clear, nevertheless. It is tentatively accepted, however, as an apomorphous feature for the family.

8. Supraorbital foramen: This leads through to the orbit and is on the base of the postorbital bar or homologous area where this is absent. As such it is well developed in *Pteropus*, *Lavia*. It is present in modified form in *Cyttarops* (Starrett and de la Torre, 1964, p. 55, figs 8, 9), and is also present in *Cynocephalus*. With additional widespread occurrences outside the bats it can be considered a primitive mammalian character and its loss derived.

9. Position of lacrimal foramen: This may open in the orbit (in) or anterior to the orbit on the side of the face (out). The primitive condition for bats is unclear.

10. Length of snout: Meaning here the general region of the skull in front of P^4 to the nasal openings.

11. Pterygoid region length: In long-skulled forms the pterygoid flanges lie even or anterior to the front of the glenoid surfaces; in short-skulled forms they lie posterior to them.

12. Inflated cranium: The inflation of particular areas of the cranium over the primitive condition. The resulting morphology is correlated with reduced ossification of the skull whereby the bone is more closely molded over the brain. Inflation, when present, appears nowhere distinctive enough to be used to form possible sister groups.

13. Inflation and exposure of semicircular canals: See p. 19. Primitively the occipital and squamosal wrap around the mastoid petrosal leaving the semicircular canals inside the skull cavity. The mastoid petrosal contributes to the surface of the skull to differing degrees in various genera of both microchiropterans and megachiropterans. It is also inflated as in the smaller emballonurids in several species of *Taphozous*, and more or less so in *Nycteris*, *Rhinolophus*, and *Tadarida*.

14. Upper incisor count: The third, I^3 (of the eutherian count), is lost for the whole family, according to Miller (1907, pp. 27, 88, 93) and others. Loss also occurs in: *Boneia*, *Rhinolophus*, *Lasiurus*, *Tadarida*, *Hipposideros*, *Rhinopoma*, *Noctilio*, *Craseonycteris*, and many others. See p. 9 on further loss of an incisor.

15. Upper premolar count: It is probably the middle P which is lost from the primitive family count, since it is double-rooted. Reduction of premolar count also shown by: *Furipterus*, *Pteronotus*, *Mormoops*, *Glossophaga*, *Nycteris*, *Eptesicus*, *Vespertilio*, *Artibeus*, *Rhinopoma*, *Noctilio*, *Lavia*, *Craseonycteris*, and others.

16. $P^{anterior}$: The vestigial premolar in Recent emballonurids is relatively larger in *Taphozous* and *Saccolaimus* and relatively smaller in other genera though variable in form and detail.

17. Hypocone distinct: See p. 13 for description. The primitive emballonurid condition is also seen in *Noctilio*, *Lavia*, *Chilonycteris*, *Thyroptera* (M^1 only), among others. The con-

fluence of the protocone and hypoconal basins to the extent seen in the large emballonurids seems to be uncommon. In several genera (e.g., *Nycteris*, *Rhinopoma*) where the hypocone is not a distinct cusp, the hypoconal basin is much lower than the protocone and the postprotocrista may be distinct.

18. Parastylar area on M^1: See p. 13 for description. The parastyle and stylocone are considered well developed when they are as high or higher than the paracrista (as seen in direct lingual view); reduced when they are lower than this. The well-developed condition is very widespread among chiropterans with dilambdodont molars, but reduction also occurs in *Micronycteris*.

19. Anterior cingulum on M^1: The primitive condition is cingulum present. However, a variety of degrees of development are observed both within and outside the Emballonuridae. In general the smaller emballonurids have a sharp, complete, well-defined anterior cingulum, although this may be accentuated by a wear groove between it and the face of the paracrista. In the larger forms it is a finer structure but distinctly present (*Saccolaimus* excepted). Absence of the cingulum also occurs in *Nycteris*, *Noctilio*. Nonemballonurid genera having the cingulum show less well-developed states than that seen in the smaller emballonurids.

20. Metacone on M^3: See p. 13 for description. The widespread primitive condition is metacone present; derived condition, absent. The metacone on M^3 is also lost in: *Nycteris*, *Lavia*, *Micronycteris*, *Lasiurus*, *Craseonycteris*, and others. It is nearly lost in *Rhinopoma*, but a small cusp is present connected to the mesostyle by a reduced ectoloph and to the protocone by a posterolingual cingulum. (See also Slaughter, 1970.)

21. Reflected ascending ramus and angle of jaw: Megachiropterans seem to exhibit the primitive pattern of having these parts of the jaw more or less in a single plane with the dentary ramus (compare carnivores, lipotyphlan insectivores, dermopterans). In microchiropterans both ascending ramus and angle are slightly reflected laterally (= moderate depth of massoteric fossa). This pattern is further accentuated in the smaller emballonurids, and also in: *Mystacina*, *Nycteris*, *Rhinolophus*, *Noctilio*.

22. Lower incisor count: The third, I_3, is lost, according to Miller (1907, pp. 24, 93). Loss of a lower incisor also occurs in: Pteropidae, *Rhinolophus*, *Phyllostomus*, *Hipposideros*, *Rhinopoma*, *Desmodus*, *Craseonycteris*, and others.

23. Separate opening associated with foramen ovale: In the primitive condition there is a single, simple, large opening from the cranium—the foramen ovale. In several genera within the family, however, there is a second opening; this is presumably the derived condition, but several morphologies are present (fig. 10). It is not clear which of these derived conditions are homologous, if any; and the distribution of possible homologies conflicts with that of other characters, making this an unsatisfactory character on the whole.

RELATIONSHIPS OF EMBALLONURID GENERA: DISCUSSION

Figure 11 presents a hypothesis of relationships for the genera of fossil and Recent emballonurid bats as represented by material investigated in this study. This hypothesis is suggested as an improvement over previous statements on

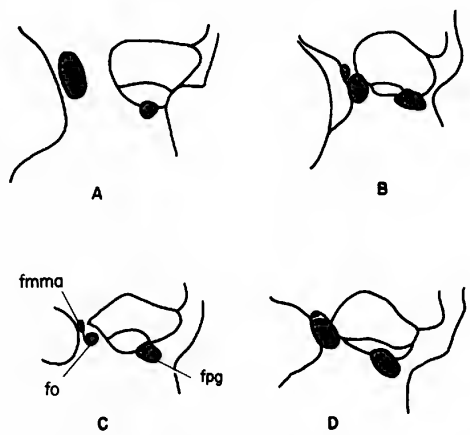

FIG. 10. Variation in the opening of the foramen ovale. A. *Taphozous nudiventris*, AMNH (Mam) 27391. B. *Peropteryx kappleri*, AMNH (Mam) 239076. C. *Emballonura sulcata*, AMNH (Mam) 87188. D. *Saccopteryx bilineata*, AMNH (Mam) 210488. Ventral views. Camera lucida drawings. A approx. ×3; B-D approx. ×5. Abbreviations, pp. 2-3.

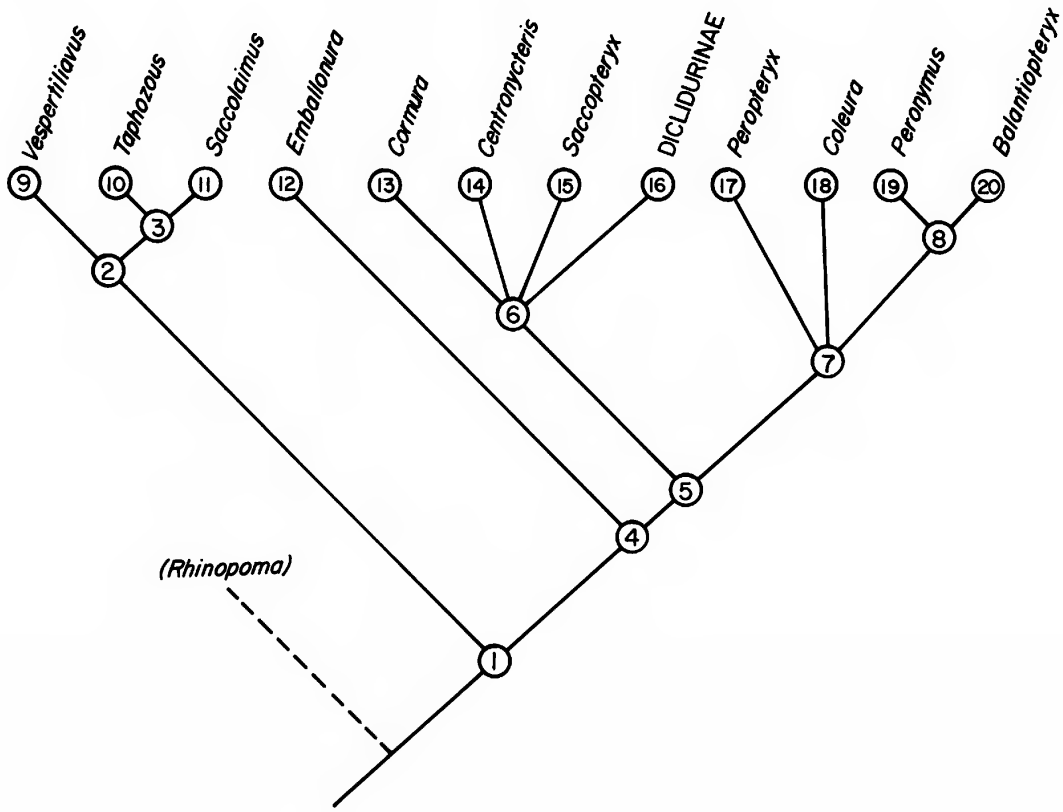

FIG. 11. Hypothesis of relationships among emballonurid bats based on characters in table 2 and the discussion, p. 23. Numbers refer to shared derived characters, table 3.

emballonurid taxonomy (e.g., Miller, 1907; Sanborn, 1937; Koopman and Jones, 1970) in that it attempts (1) to use as many characters as can be discerned in the morphology of the skull, and (2) to specify as exactly as possible degrees of relationship among the genera or groups recognized as OTUs. Previous work has relied on standard taxonomic working methods of using characters for diagnostic purposes only without always assessing their phylogenetic significance (i.e., degrees of apomorphy and plesiomorphy); and of not assessing the significance of, or possible solution for, conflicting character distributions.

The cladogram may be summarized as follows. As regards major relationships within the family, the genera group into four monophyletic clades, in two of which there are problem areas expressed as trichotomies. The first of these clades consists of the genera *Peropteryx*, *Coleura*, *Peronymus* and *Balantiopteryx*—those emballonurids characteristically with single median basisphenal pits. The genera *Cormura*, *Centronycteris*, *Saccopteryx*, and the subfamily Diclidurinae (includes genera *Diclidurus*, *Cyttarops*, and *Depanycteris*) are, collectively, more closely related to the single pit forms than to any other emballonurid. *Emballonura* alone comprises the third monophyletic clade. It and, collectively, the other smaller emballonurids are equally related to the fourth clade—the large Old World genera. (The entire family may have its closest relative in the genus *Rhinopoma*; this is merely suggested without thorough inspection of the character distributions.)

The hypothesis of figure 11 fails to satisfy fully on two counts. First, neither this hypothesis nor any alternative seems to be free of mul-

TABLE 3

Explanation of Characters Used in Figure 11

1. Reduced premaxillaries, absence of palatine portion, etc. (see p. 21).
   Presence of basisphenal pits (extent and form variable).
2. Basisphenal pits of characteristic shape and size.
   Loss of distinct hypocone on posterolingual cingulum of M^1 and M^2.
   Confluence of protoconal and hypoconal basins.
   Large size.
3. Loss of second premolar (of primitive bat formula).
   Shortening of snout.
   Loss of one lower incisor.
   Loss of one upper incisor.
   Hypertrophy of foramen for ?mandibular-alveolar vein.
4. Loss of supraorbital foramen.
   Shortening of pterygoid region of skull and of face (distance between C and P^{last}).
   Inflation and exposure of semicircular canals and pars mastoideus on posterolateral surface of skull.
   Accentuation of reflection of ascending ramus and angle of jaw.
   Loss of second premolar (of primitive bat formula).
   Loss of parastylar area on M^1.
   Presence of nasomaxillary inflations.
5. Loss of one upper incisor.
6. Hypertrophy of cochlear process of basisphenoid (see p. 16).
7. Single median basisphenal pit (note: slight indications of lateral pterygoid pits often associated; whether these two features are always correlated is unclear).
8. Hypertrophy of canal opening in roof of interpterygoid region near border of basisphenal pit.
9. Wide separation of basisphenal pits.
   Hypertrophy of grooves on snout communicating from supraorbital foramina (p. 9).
   Absence of recessed dorsal narial border (p. 8).
   Extensive cheek area [for origin of buccinator musculature].
10. Nasal depression of characteristic form anterior to bifurcation of sagittal crest.
    Loss of supraorbital foramen.
11. Accentuated breadth of skull, especially across zygomatic arches.
    Completely ossified auditory bulla.
    Loss of nasal depression, flat to convex snout.
    Posterior extension of sagittal crest beyond posterior cranial wall.
    Hypertrophy of cochlear process of basisphenoid (see p. 16).
12. Nasomaxillary inflations leaving median nasal area furrowed.
13. [None].
14. Separate opening close to foramen ovale (but see table 2 for distribution).
15. Very large supramastoid foramen between mastoid and exoccipital bones.
16. Paired nasal depressions and associated bony protuberances in circumorbital region, consisting of modified premaxillaries.
17. Accentuated nasal inflations in maxillary bones.
18. [None].
19. Dorsal narial border: straight and not indented.
20. Hypertrophy of lateral pits associated with median one, separated by partial bony septum and bordered by bases of pterygoid flanges (also occurs on some species of *Emballonura*).

tiple evolution of features or complicated evolutionary histories. The emballonurids fall at a glance into two distinct groups or morphotypes, namely (1) large, mostly long-faced, heavy built forms; (2) small, short-faced, lightly built forms. Although the fossil *Vespertiliavus* belongs to the former group, it is not clear which morphotype is the more primitive. The large forms have here been defended as the more primitive largely on the basis of the dental formula of *Vespertiliavus*. That is to say, a premolar count of three is taken to be primitive for the family; all the smaller forms are therefore derived with respect to *Vespertiliavus* (fig. 11, character 3 in part). However, this character may not correlate with the large, long-faced morphotype. As with many other features, comparison outside the family (e.g., *Noctilio*, *Rhinopoma*, and others) is ambiguous: both long-faced and short-faced morphotypes are widespread among Mega- and Microchiroptera. There is also the problem that *Emballonura*, of the short-faced, light-skulled morphotype, has a primitive dental formula (table 2, no. 12). Assuming that both (i) 2 upper incisors, and (ii) 3 upper premolars are primitive conditions, the following hypotheses may be advanced:

1. Emballonurids primitively had short-faced, lightly built skulls, as in *Emballonura*. This implies three independent losses of P^3 and a single loss of a lower incisor (fig. 12A).

2. Emballonurids primitively had long-faced, heavily built skulls, as in *Vespertiliavus*. This implies two independent losses of P^3 and two independent losses of a lower incisor (fig. 12B).

The second hypothesis is preferable because it involves less parallelism in the evolution of P^3 and because there is the possibility (contrary to Miller, 1907, however) that the incisors lost in the two clades may not be the same.

A second problem involves *Centronycteris*, *Saccopteryx*, and *Cormura*. These and the Diclidurinae appear to share a derived character (albeit independently acquired in *Saccolaimus* and some *Taphozous* species) in the hypertrophy of the cochlear process of the basisphenoid. However, as seen in table 2 every possible synapomorphy used to pair two of these forms to the exclusion of the others, or to combine three to the exclusion of one other, conflicts with other possible synapomorphies that imply alternate groupings. There appears to be no way to arrive at a least objectionable synthesis; all four groups remain, therefore, as separate OTUs in uncertain relationship. Several possible derived characters are shared by one or another of these with the clade of single pit forms. But again, any one arrangement involves multiple evolution of some characters. This difficulty is not new in the taxonomy of the family; these genera, with some others, have been described as close cousin genera ("Genres cousins" Brosset, 1966, p. 170), and have even been synonymized (Simpson, 1945, p. 55) despite their earlier recognition as separate taxonomic entities (Sanborn, 1937). Indeed they all but one have the same geographical distribution; they are all very similar in morphology generally. Only the diclidurines are distinctly different. They possess deep nasal depressions [accentuated more in *Diclidurus* and *Cyttarops* than in *Depanycteris* (Thomas, 1913, 1921)] and associated unique morphology. Not surprisingly the three genera have been accorded subfamily rank within the Emballonuridae (Koopman and Jones, 1970; and others). As interpreted here, the nasal depressions are merely a striking autapomorphy; other cranial features in these three genera are either primitive for the family or shared with perhaps some, perhaps other genera.

The presence of a single median basisphenal pit is taken to be homologous among the genera *Peropteryx*, *Coleura*, *Peronymus*, and *Balantiopteryx*. Development of pterygoid pits to some degree is present in all these genera as well, and their hypertrophy can be used to relate two of them to the exclusion of the other two. However, no consistent character can be found to relate three forms to the exclusion of the fourth or to relate as sister groups the two forms not exhibiting well-defined pterygoid pits. Some species of *Emballonura* (notably *E. nigriscens*, *E. raffranyana cor*) exhibit pit morphology quite similar to that seen in *Coleura* and *Peronymus*. *Emballonura beccarrii* possesses a broad, shallow basicranial depression of trapezoidal shape, unlike any other form in the family. *Emballonura sulcata* has very reduced paired pits. (Variation in pit morphology in the genus is figured by Tate and Archbold, 1939, p. 3, fig. 2.) On the basis of this character alone it might be suspected that

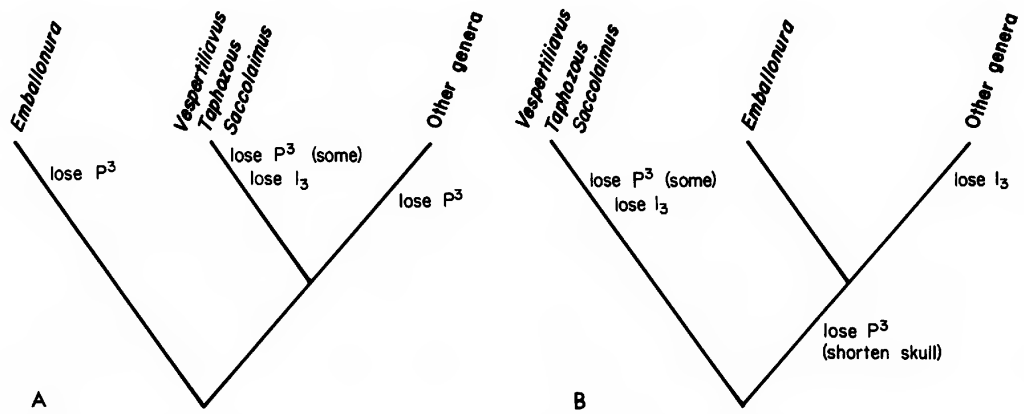

FIG. 12. Alternative hypotheses for the evolution of the dental formula in emballonurids. See p. 26 for discussion.

Emballonura is an unnatural group, that some species might be reassigned among other genera. It is retained here because (1) such revision would entail multiple loss of the upper incisor (i.e., character 5, fig. 11 would be invalidated), and (2) all species of *Emballonura* examined characteristically exhibit a median furrow on the snout between naso-maxillary inflations (see also Miller, 1907, p. 87). This character is taken to be a valid autapomorphy for the genus.

SUMMARY AND CONCLUSIONS

1. New material of the early Tertiary genus *Vespertiliavus* Schlosser has been described to show the extended range of morphology, and more complete picture, of this form which has been brought to light. *Vespertiliavus* is on the basis of shared derived characters more closely related to the *Taphozous-Saccolaimus* group of living emballonurids than to other members of the family and is not regarded as ancestral to the family as a whole (as was correctly noted by Revilliod, 1920, pp. 100-101). Indeed it appears that the smaller emballonurids may exhibit a majority of the features primitive for the family (contrary to Revilliod, 1920, p. 100).

2. Skull characters have deliberately been emphasized not only because of the nature of the fossil material but also to ascertain the extent of their usefulness for bat systematics both below and at the family level. A limited number of characters do appear to be useful in this way. It is, however, clear from table 2 and the discussion on pp. 23-26 that such morphology has not entirely clarified relationships within the family Emballonuridae. It has, nonetheless, led to a specific hypothesis on those relationships and pointed to several areas in particular which require some refinement. Obviously reference to associated postcranial morphology should be made.

3. The discussion on pp. 19-23 has shown also that skull morphology among chiropterans generally will yield many cases of conflicting character distributions, that is, will require postulating numerous cases of independent acquisition of features. This may be true among OTUs at both the genus and family levels. Under the circumstances, cladistic analysis may be the most objective approach to sorting out these conflicting character distributions and to wielding the large number of named taxa. In dealing with these problems the traditional higher level taxonomy of bats has seemingly wavered between two equally unsatisfying solutions. In one instance workers have recognized an excessive number of distinct but unclearly related taxa, often of fairly high rank (monospecific families) to reflect the inconsistent appearances or irregular combinations of characters (e.g., Hill, 1974, p. 305). In response, others have synonymized extensively to maintain a workable number of OTUs in an attempt to see broader relationships. (See Simp-

son, 1945, p. 180 for criticism of the former and advocation of the latter case.) While making preliminary assertions about the primitive or derived nature of certain characters, such traditional methods tend not to conclude in an accessible manner which groups among the bats are natural monophyletic assemblages and how much relationships among others has been obscured by convergent evolution. The search for groups which are wholly primitive has not been successful, for few exist which do not exhibit some derived features or autapomorphies [e.g., relations of the Pteropodidae or *Rhinopoma* (Koopman, 1967, pp. 116, 117); of *Vespertiliavus* itself]. If indeed bats have been notoriously parallelistic in their evolution, cladistic analysis will provide explicit statements as to which characters may have evolved more than once and are not homologous where they are seen, which may be defended as validly relating groups of closest common ancestry. Competing hypotheses may then be assessed with the assurance that they have been arrived at through comparable methodology. The present study has indicated that the situation is challenging but potentially workable by this approach.

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